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Changes in the terrestrial chironomid community (Diptera: Chironomidae) during secondary succession in old fields

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Summary. Community structure, larval abundance and emergence phenology of terrestrial Chironomidae (Diptera) were studied in three stages of a secondary succession in the Czech Republic between 1986–1992: a cultivated field (plot A), a fallow field – abandoned in 1985 (plot B) and a meadow – originally also a field but abandoned between 1975–1977 (plot C). Seven, nine and ten species respectively were recorded from these plots. The highest larval abundance was found in plot A and reached 1480 individuals m^{-2} in November 1988. In plot B, the fallow field, abundance was greatest during the earlier stages of succession and declined in the second year of succession. The lowest abundance was found in the meadow (plot C). Vegetation structure and soil moisture were found to be the main factors affecting chironomid density.

Key words: Diptera, Chironomidae, soil fauna, long-term study, secondary succession

Introduction

The larvae of aquatic Chironomidae play an important role in colonization of newly flooded ponds (Matěna 1990). The larvae of terrestrial Chironomidae are also recorded as a dominant group of edaphon in the early stages of secondary (Strüve-Kusenberg 1981) or primary (Trehen et al. 1987) successions. However, in most ecological studies, terrestrial Chironomidae have only been identified down to the family level. Thus, we have little information about the role of particular species during the course of succession in terrestrial habitats. Some information about habitat preference of terrestrial Chironomidae were given by Strenzke (1950). Successional changes in the Chironomidae community after prescribed fires were studied by Delettre (1989). The aim of this study was to answer the following questions: 1) How does a chironomid community change during the course of secondary succession in fallow compared to an agriculturally managed field and an unmown meadow? 2) Which environmental parameters were responsible for these changes?

Materials and Methods

Site description

The study area is located in South Bohemia, near Vodňany, 570 m a.s.l. (49°6' N, 14°7' E). The soil type is entric cambisol (Němeček & Tomášek 1983). The average annual temperature is 7.3 °C and mean annual rainfall 605 mm. Soil moisture and climatic changes during the course of the study are given in Fig. 1. Soil moisture is expressed as % of dry mass. The chironomid larval communities were studied in three plots. These plots represented different stages in a secondary succession.

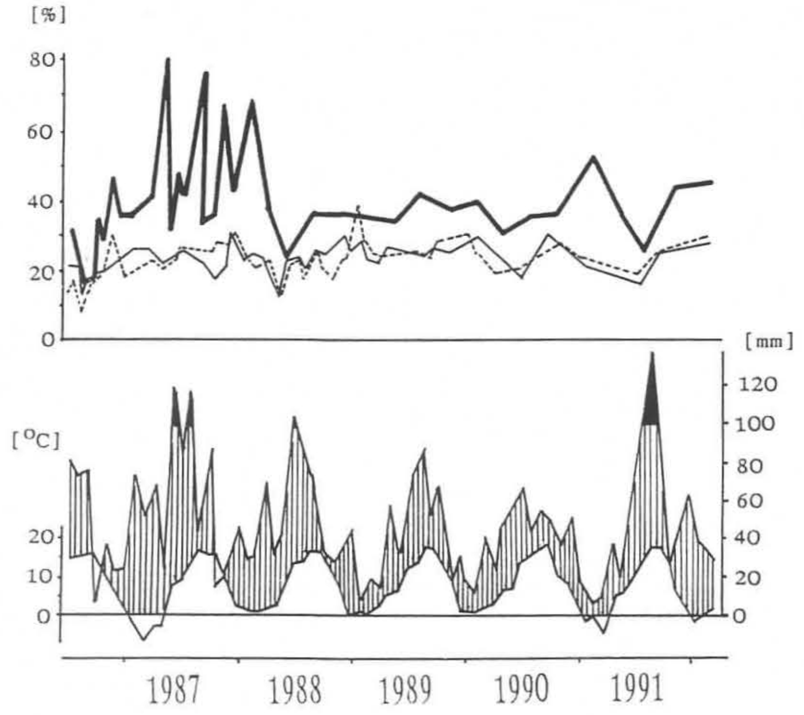

Fig. 1. Moisture changes in the studied plots (field: interrupted line, fallow: full line, meadow: bold line) and climatic – diagram of monthly temperature and rainfall fluctuation (below)

Field: The first plot (A) (15 × 150 m) was a cultivated field. Soil pH was 6.3 (H_2O 1 : 2.5) (Matějka, 1990). Agricultural practices until November 1990 are summarised in Fig. 2. After this period, there was no further cultivation. The dominant plant species in the resulting early fallow were *Cirsium arvense* (L.) Scop. and *Rumex obtusifolius* DC.

Fallow: The second plot (B) was a fallow (15 – 20 m × 200 m) which was originally part of the cultivated field described above. Agricultural practices were stopped in 1985 and changes in the vegetation of this plot during the course of succession are given in Tab. 1.

Meadow: The third plot (C), a meadow (70 × 100 m), was previously arable land. It was abandoned between 1975 – 77 and it was mown regularly until 1985. This was the wettest of al the studied plots. The soil type is gleic cambisol. The plant community was dominated by *Holcus mollis* L. (Matějka 1990). In 1990, the layer of grass litter on the surface was 3 – 5 cm thick.

Sampling

Larvae: A sampling area (10 × 10 m) was marked on each plot. Five soil samples were taken from each sampling area (4 in each corner and 1 in the middle) on each sampling occasion by means of a circular sampler (working area 625 cm^2) to the depth 10 cm. The soil fauna was extracted using high gradient extractors. The material was fixed in 4% formaldehyde and preserved in 75% ethanol. Soil sampling was performed from 1986 to 1992. Starting on the 7th May, 1986 samples were taken every 4 weeks for two years, and 4 times a year (in February, May, August and November) in the following years.

Adults: Adult emergence was studied for one year (April 1991 – March 1992) using 3 emergence traps (working area 0.25 m^2) on each plot. Imagos were fixed in a collector with 4% formaldehyde. During winter, glycerin was added to prevent freezing. Except for a winter pause (28. 11. 1991 to 6. 2. 1992) material from the traps was collected every 3 weeks, then the traps were moved to a new location.

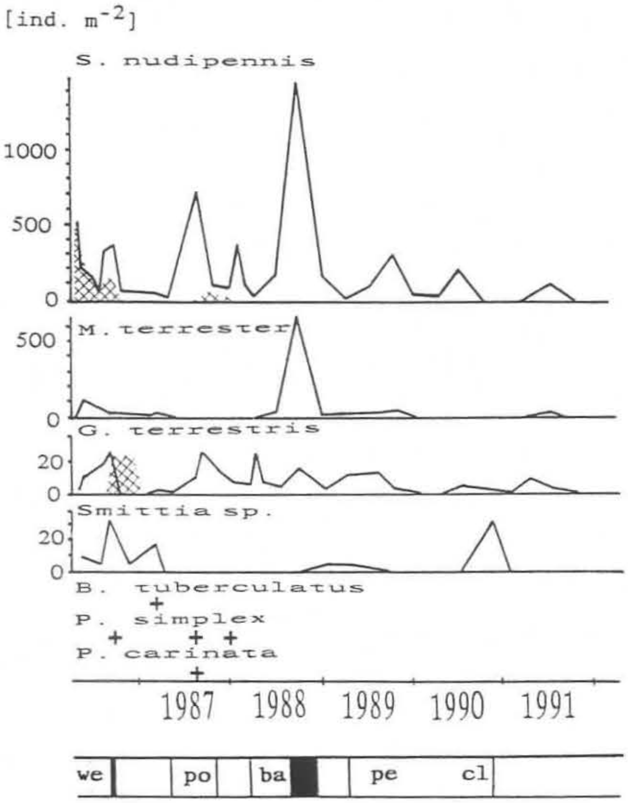

Fig. 2. Abundance fluctuation of chironomid larvae and pupae in the field. Shaded area = abundance of pupae multiplied by ten. for rare species only the presence of larvae in soil is noted = +. At the bottom the scheme of cultivation on the field is given. White area with letters = soil with plant culture (w wheat. po potatoes. cl clover. pe peat and oats. ba barley). black area without letters = field after tillage. white area = field after ploughing

Table 1. Changes of vegetation cover on the fallow (plot B)

year	1986	1988	1989
percentage of covered soil surface	75	95	100
number of plant species	43	33	22
plant biomass [$g \cdot m^{-2}$]			
live	267	334	343
dead	19	260	474
Apera spica-venti (L.) Beauv.	4		
Myosotis arvensis (L.) Hill.	2		
Plantago uliginosa Schmidt	2		
Fallopia convulus(L.) Love	1		
Rhaphanus rhaphanistrum L.	1		
Viola arvensis Murray	1		
Agrostis capilaris L.		3	1
Cirsium arvense (L.) Scop.	+	3	3
Epilobium ciliatum Rafin	+	3	3
Calamagrostis epigéos Roth.		2	4

Note: + rare species. 1 species with dominance to 5%. 2 dominance 5–25%. 3 dominance 35–50%. 4 dominance 50–70%. after Matějka (1990)

Determination

For the study of morphological details, slides for light microscopy and gold coated specimens for SEM were prepared. Larvae were determined to the species level or to groups of species using the keys provided by Strenzke (1950), Moller-Pillot (1984) and Cranston, Olivier & Saether (1983). The key by Coffman (1986) was used for determination of pupae. Adult determination was carried out using Pinder (1978).

Data processing and statistics

The linear regression (in normal or log normal scale) was used for studying the relationship between fluctuations in average annual abundance and soil moisture (r = regression coefficient). May to May periods were considered as a year for this purpose. The data from all sampling occasions of the appropriate year were used for calculation of annual average abundance. Diversity (H) (Shannon & Weaver 1963) and equitability (E) (Sheldon 1969) indexes were used. Dominance (D) is expressed as the species percentage of the total of the recovered larvae.

Results

Chironomid communities

A total of ten species were recorded in the three studied plots: *Bryophaenocladius tuberculatus* (Edwards, 1929), *Gymnomertiocnemus terrestris* (Goetghebuer, 1941), *Metriocnemus fuscipes* (Meigen, 1818), *Metriocnemus inopinatus* (Strenzke, 1950), *Metriocnemus terrester* (Pagast, 1941), *Parasmittia carinata* (Strenzke, 1950), *Pseudorthocladius curtistylus* (Goetghebuer, 1921), *Pseudosmittia simplex* (Strenzke-Thieneman, 1942), *Smittia nudipennis* (Kieffer, 1922), and *Smittia* sp.

Field (Plot A): The maximum abundance of chironomid larvae reached 1480 ind. $\times$ m^{-2} (10. 11. 1988). This was the highest value of actual abundance in all studied plots. Also the annual average abundance (38.4 – 448.4 ind. $\times$ m^{-2}) was the highest here of all plots studied.

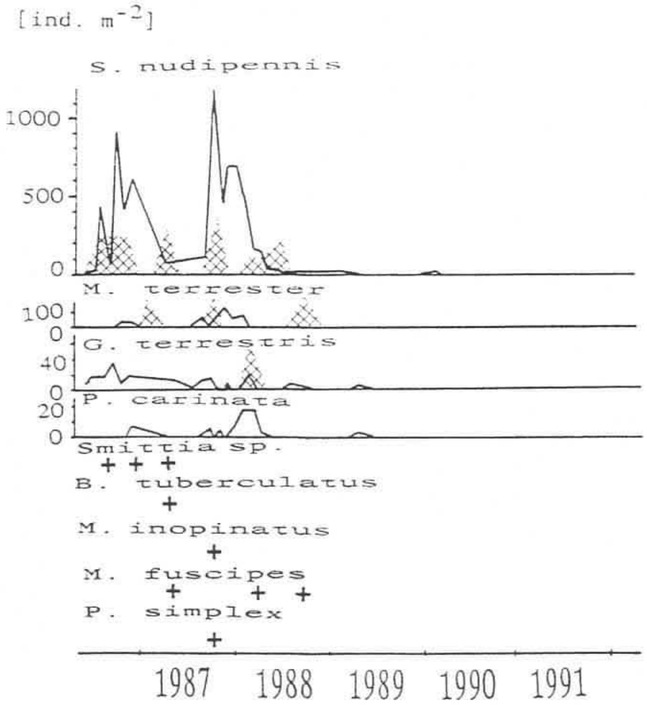

Fig. 3. Abundance fluctuation chironomid larvae and pupae in the fallow. Shaded area – abundance of pupae multiplied by ten, for rare species noted only presence of larvae in soil = +

The community was composed of seven species (Fig. 2) with *Smittia nudipennis* being most abundant. The high dominance of *S. nudipennis* (D = 90.0 – 48.0%) accounts for the low diversity and equitability index value (H = 0.51 – 1.03 bit. ind^{-1}, E = 0.32 – 0.51). In the years 1988 – 1990, when clover was growing in the field, the abundance of *Gymnometriocnemus terrestris* and *Metriocnemus terrester* increased, which resulted in higher diversity and equitability indexes (H = 1.05 – 1.53 bit ind^{-1}, E = 0.62 – 0.76). Larval abundance peaked on two occasions: in winter and in summer, while only one winter peak was recorded in the other plots.

Fallow (Plot B): In the first two years after cultivation had been stopped, a maximum of 1160 ind. × m^{-2} was recorded (12. 10. 1987) from this plot. In the following years, the total abundance of chironomid larvae decreased below 10 ind. × m^{-2}. Nine species were established here (Fig. 3). As in plot A, *Smittia nudipennis* was dominant (D = 70.0 – 90.0%), and only two other species were common: *Gymnometriocnemus terrestris* (D = 2.3 – 15.0%) and *Metriocnemus terrester* (3.2 – 10.0%). Diversity and equitability were low (H = 0.65 – 1.45 bit. ind^{-1}, E = 0.21 – 0.94). The increase of equitability in the last years was caused by a decrease in total abundance and not by an increase in species number.

Meadow (Plot C): Larval abundance was found to be lower in this plot than in plots A and B during the first two years of succession. Ten species were established here (Fig. 4).

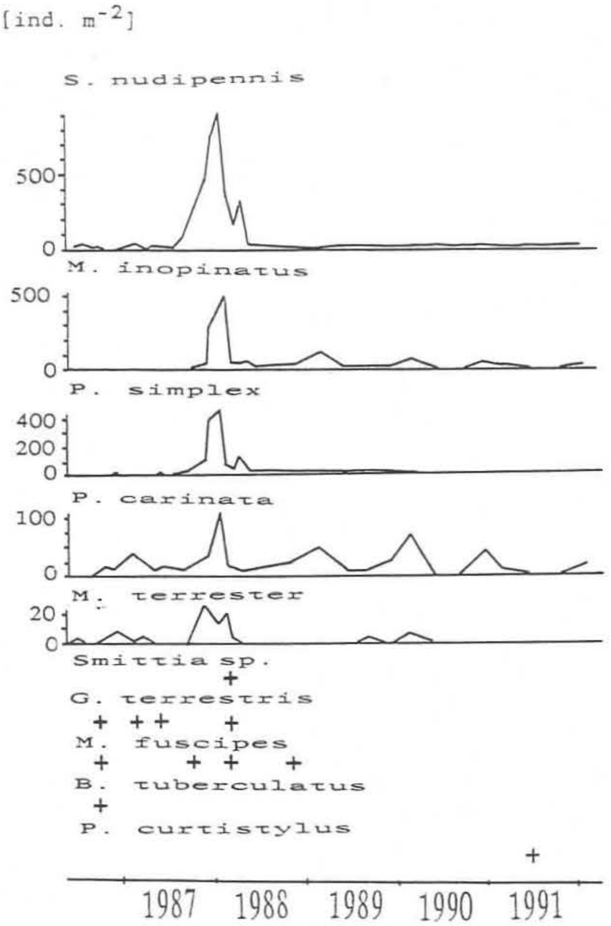

Fig. 4. Abundance fluctuation of chironomid larvae in the meadow, for rare species noted only presence of larvae in soil = +

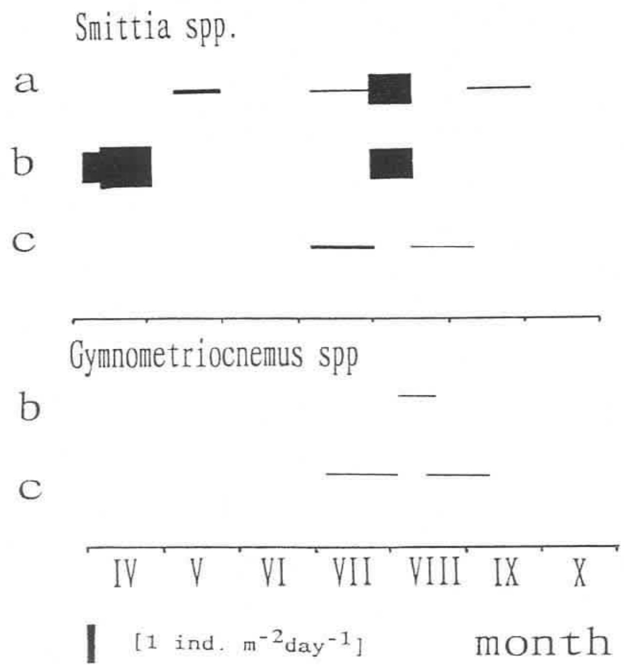

Fig. 5. Emergence of Chironomidae from the soil. a = field, b = fallow, c = meadow

Although *S. nudipennis* was the most abundant species during the first two years, its dominance values were lower than in the other plots (D = 66.0 – 57.0%). The most abundant species in the following years were *Metriocnemus inopinatus* (D = 0.0 – 54.0%), and *Parasmittia carinata* (D = 20.0 – 54.0%). Diversity (H = 1.51 – 1.95 bit. ind^{-1}) and equitability (E = 0.55 – 0.91) were highest on the meadow plot.

Adult emergence and life cycles

The presence of pupae in the soil (Fig. 2, 3) suggest, that there are two generations per year in *S. nudipennis*. Adult emergence phenology (Fig. 5) give similar results. A total of 48 adults of *S. nudipennis* and 5 adults of *G. terrestris* were trapped. The winter generation of *S. nudipennis* larvae emerge in May and adults of the summer generation emerge in August and early September. The same pattern is suggested by catches of pupae in soil cores for *G. terrestris* and *M. terrester* but the emergence of adults of the winter generation seems to occur earlier than for *S. nudipennis*.

Chironomid community and environmental changes

Vegetation: In the course of the succession on the fallow, the chironomid abundance decreased (Fig. 3). The changes in chironomid abundance correspond with those of the plant community: The annual weeds (dominated by *Apera spica-venti*) were replaced by tenacious grass (mainly *Calamagrostis epigeos*, Tab. 1) during the succession. Due to these changes the spatial structure of plant cover was changed and the amount of litter increased. On the other hand, the presence of an annual weed community in the field (plot A) in 1988, due to late ploughing (25. 11. 1988), caused an increase in chironomid abundance (Fig. 2).
The relation between the type of vegetation structure (see Table 2 for the description of vegetation types) and abundance of the winter generation of larvae is apparent from Fig. 6. Significantly higher (P = 0.95) numbers of *S. nudipennis* larvae were observed on the plots

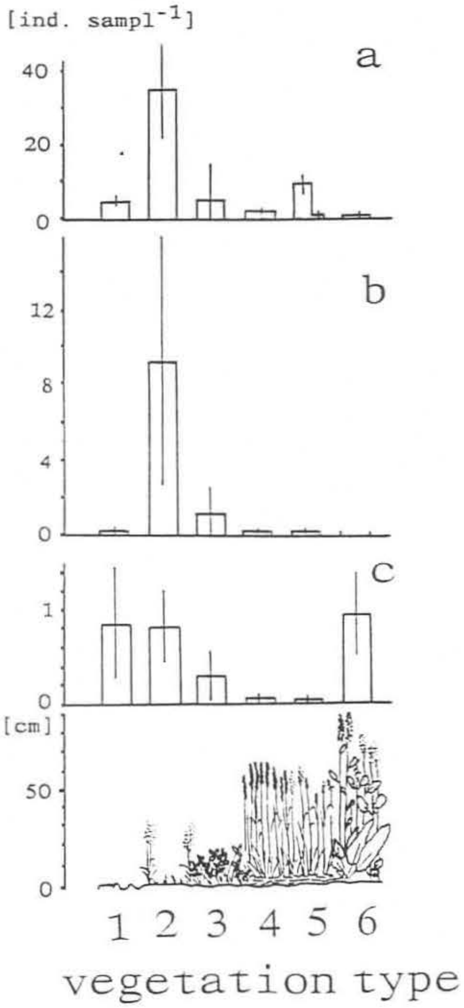

Fig. 6. Relation between vegetation type and amount of chironomid larvae per sample unit in winter samples for *Smittia nudipennis* = a, *Metriocnemus terrester* = b and *Gymnometriocnemus terrestris* = c. In each year the November and February samples were used. The average value (columns) and confidence interval (P = 0.95) (bars) are indicated. For *S. nudipennis* in vegetation type 5 the left part of column is based on all set data, right with disregard of data from extremely wet year

with annual weeds (vegetation type 2) than on all other plots (Fig. 6a). The lowest abundance was found in the plots with tall vegetation (types 4, 5, 6). The high abundance of *S. nudipennis* on the meadow is possibly due to the high soil moisture in this plot. If we disregard the data from the extremely wet year (1987—88), no significant differences were observed among all types of tall vegetation (Fig. 6a). The larval abundance on the plots after ploughing (type 1) is higher than on the plots with tall vegetation and lower than in the plots with annual weeds. Both differences are significant (P = 0.95). A similar correlation was established between vegetation and abundance of *M. terrester* lavae, which appeared to be more affected by ploughing (Fig. 6b). The trends described above are not so apparent in *G. terrestris* (Fig. 6c), probably because of the small number of larvae extracted.

Soil moisture: Soil moisture seems to be the principal factor affecting changes in larval abundance in the meadow (Plot C). However, annual average soil moisture is not significantly correlated (r = 0.422) with the abundance of chironomid larvae, but soil moisture at the time of egg laying of the winter generation shows a significant positive correlation with chironomid abundance. The following relationships were found between soil moisture in September (m) and the annual average of chironomid abundance on the meadow (a):

for the whole community
$a = 1.264\,m - 312.75$ $(r = 0.948)$
for *Smittia nudipennis*
$a = 6.912\,m - 211.86$ $(r = 0.945)$
for *Metriocnemus terrester*
$a = 1.877\,m - 53.31$ $(r = 0.967)$
for *Parasmittia carinata*
$a = 16.1059\,(\ln m) - 43.159$ $(r = 0.717)$
for *Pseudosmittia simplex*
$a = 2.592\,m - 82.254$ $(r = 0.964)$

Table 2. Types of vegetation structure observed during the course of succession on the fields near Vodňany (Czech Republic)

No of vegetation type	description
1	soil without plants after ploughing;
2	soil one or more years after ploughing, the dominant plant species are *Apera spica-venti* and other annual weeds; small amount of litter (up to 300 g m^{-2});
3	culture of clover with weed (*Cirsium arvense* and *Rumex obtusifolius*); intermediate group between types 2 and 4;
4	taller species of grasses; large amount of litter (more than 300 g m^{-2}); the dominant plant species is *Calamagrostis epigeos*;
5	the taller species of grass; large amount of litter (more than 300 g m^{-2}); the dominant plant species is *Holcus mollis*;
6	tall vegetation of weed (mainly *Cirsium arvense* and *Rumex obtusifolius*); without litter.

Discussion

The larvae of Chironomidae were found to be most abundant in the field and fallow during the early stages of succession corresponding with data of Strüve-Kusenberg (1981). Three species account for 98% of the chironomid community: *M. terrester*, *G. terrestris* but mainly *S. nudipennis* (up to 90% of the total abundance). A similar pattern in larval chironomid communities was recorded for Swedish agricultural fields (Delettre & Lagerlöf 1992). The meadow species were recorded by Strenzke (1950) from mosses and wet meadows.

The emergence of adults and the occurrence of pupae and adults in the soil samples suggest that there are two generations of the three main species (*S. nudipennis*, *M. terrester* and *G. terrestris*) during the year. The first generations emerged in spring, and the second in late summer. Similar bivoltine life-cycles were recorded by Delettre & Lagerlöf (1992) and Seddon (1986) for *Smittia aterrima* (Meigen, 1929).

Seasonal dynamics seem to differ on the three plots: in the fallow (plot B) and meadow (plot C) only the winter peaks of abundance were observed, whereas in the field (plot A) both a winter and a summer peak of larval abundance were found. The adults emerging from the field are likely to disperse over the other plots. A recolonisation pattern like this was observed in adjacent heterogeneous habitats on heathlands in Brittany (Delettre 1986). Fluctuations in larval abundance in the meadow (plot C) appeared to be controlled by soil moisture during the oviposition period. Soil dryness negatively affected egg-laying and resulted in low larval abundance in the meadow. Larvae of terrestrial Chironomidae show some behavioural adaptations which enable them to resist soil desiccation, these include vertical migration and cocoon building (Delettre 1988). Such capabilities are probably very limited in younger larvae and adequate moisture should be the main factor limiting their survival. Older larvae probably do not depend so closely on soil water content and. in addition. large amounts of water in the soil can be harmful for prepupal stages (Blanchard et al. 1987). In view of this. it is not surprising that the annual average soil water content showed no significant correlation with larval abundance.

The structure of vegetation was found to be the primary factor affecting successional changes in chironomid communities. The relationship between vegetation structure and larval habitats is well known for some Ceratopogonidae (Maghon et al.. 1990). As was shown by Delettre et al. (1992). vegetation patterns affect the aerial dispersal of terrestrial Chironomidae and. vegetation structure can modify the numbers of females invading certain habitats for egg-laying. In addition. in the meadow. egg-laying success could have been affected by the heavy litter layer. which prevents the eggs from making direct contact with the soil capillaries. Hövemeyer (1992) reported on a decrease of chironomid abundances in plots of a beech forest soil. where litter was artificially added. However. it is not only the presence of tall vegetation and a litter layer that affected larval populations negatively but. also. the bare field immediately after ploughing seems to be unsuitable for the development of larval Chironomidae. This is probably caused by the poor moisture condition in the soil surface layer. Accordingly Delettre & Lagerlöf (1992) suggested that this factor might be responsible for low Chironomid abundances in Swedish crop fields. On the other hand. soil overwintering changes. mainly increasing of porosity and better water saturation. (Unger 1991) can be the reason why the summer larval generation are more successful in this plot.

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